LIFE HISTORY OF FOSSOMBRONIA CRISTULA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 264

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(WITH PLATES XIV–XIX AND ONE FIGURE)

Fossombronia, according to SCHIFFNER (8), comprises 26 species of world wide distribution. The genus belongs to the family Codoniaceae of CAVERS (2), which is, next to the Haplomitriaceae, the highest family of the anacrogynous Jungermanniales. *Fossombronia* and its closely related genera *Blasia*, *Noteroclada*, and *Treubia* are thalloid dorsiventral forms which show the beginnings of genuine leaves corresponding to those of the acrogynous Jungermanniales, and represent, with the Haplomitriaceae, possible ancestral forms from which the Acrogynae have been derived.

Fossombronia cristula was discovered and named by AUSTIN (1) in 1868, who found it growing "on damp sand in an unfrequented path" near Batsto, New Jersey. For many years no additional material was collected, nor was it reported as occurring in any other locality in the United States. This no doubt was due to the small size and obscure habitat of the species. In 1915 EVANS (3) made a taxonomic study of *F. cristula* and stated that specimens had been collected in Massachusetts, Connecticut, New York, New Jersey, West Virginia, and Indiana. LAND found the species in 1914 in Porter County, Indiana, 2–3 miles east of Dune Park, and a preliminary report of its occurrence in this region was published by HILL (5) in 1916 from material furnished him by LAND. HILL also found plants growing in Lake County, Indiana, 3 miles east of Tolleston. In his paper the author incorrectly refers to the species as *F. crispula*, which is not the name given it by AUSTIN.

Material

The material used in this study to illustrate the development of the sporophyte was kindly furnished by Dr. LAND from his collection of 1914 from the Dune Park region. Additional plants

were obtained by the writer from the same locality in 1917, about a month earlier than Dr. LAND's material had been collected, and served to illustrate the development of the thallus and the sex organs. The writer found *F. cristula* in this locality growing in cracks on fine, wet deposits of silt on the bottom of an almost extinct lake. HILL notes that "a favorite place of growth in the Tolleston locality was vertical sides of holes left in the mud by the feet of cattle." In the Dune Park region the plants are associated in great abundance with *Drosera longifolia*.

Historical summary

The earliest detailed study of *Fossombronia* is that of LEITGEB (7), who investigated *F. pusilla*, a European species. The author made a very careful study of the origin and insertion of the leaves and the development of the stem axis and mucilage hairs in the region of the growing point of the thallus. The apical cell is dolabrate, cutting off alternately right and left segments only. The plants are mostly monoecious, and on those in which antheridia are in greatest abundance, archegonia also occur to a limited extent. In regard to the order of appearance of the sex organs, the author says: "Aber ich fand häufig Sprosse mit völlig entwickelten Kapseln, welche nach der Spitze hinwieder reichlich Antheridien producierten." The position of the antheridia and archegonia is the same as that of the other species, and both originate close to the apical cell. In regard to the development of the antheridia it is stated that they deviate in no way from the normal type, although no figures are shown to illustrate this development. The venter of the archegonium is 2 cells thick before fertilization.

The fertilized egg is elongated in the direction of the archegonium axis, and divides by 2 horizontal walls, forming a tier of 3 superimposed cells, of which the lower forms the foot, the middle cell the seta, and the upper one the capsule. The upper and lower cells divide more actively than the middle one. The differentiation of wall cells and sporogenous tissue in the capsular region occurs early. The mature capsule is 2-layered; the inner wall forms annular thickenings. At the apex the capsule wall is 3-layered.

The author studied the germination of the spores; he notes that a dolabrate apical cell is organized early, but he makes no statement regarding the development of the leaves.

The most complete study of *Fossombronia* since LEITGEB is that by HUMPHREY (6), who investigated *F. longiseta*, a species occurring in California. The thallus reaches a length of 30 mm. and develops genuine leaves like the other species of the genus. The plants revive well after undergoing desiccation, and tuber-like thickenings are formed on the stem in which fungi live. The plants are monoecious, or by exception dioecious. HUMPHREY'S account of the development of the antheridium is most interesting, in that it departs widely from the usual Jungermanniales type.

The initial cell of the antheridium is somewhat larger than the neighboring vegetative cells, and is readily distinguished from them by its deeper staining qualities. . . . . Just previous to the first division the initial cell becomes considerably elongated, extending a third or more of its total length above the surrounding cells. The first division results from the formation of a horizontal wall which cuts off the stalk from the antheridium itself. Unlike what occurs in the majority of the Jungermanniaceae, the next division, instead of being vertical, is horizontal, thus dividing the antheridium mother cell into two superimposed cells; whereas in *Sphaerocarpus* and *Geothallus* another horizontal wall is formed, thus producing another cell, the two uppermost dividing vertically to form the antheridium, while the basal cell, by a series of transverse walls, forms the foot.

In *Fossombronia* the development thus far agrees exactly with that in *Sphaerocarpus* and *Geothallus*, except that in *Fossombronia* only one horizontal division occurs in the antheridium mother cell, the stalk arising from the basal cell formed by the first horizontal division. This basal cell later divides horizontally, the uppermost segment becoming active in the formation of the stalk, while the lower ordinarily does not divide again. Following the horizontal division of the antheridium mother cell are two vertical divisions forming planes at right angles to each other and dividing the antheridium into octants. The next division results in periclinal walls for each of these octants, and there thus arise eight central cells and eight periclinal ones. . . . .

Judging from the development of the antheridium, *Fossombronia* is more closely related to *Sphaerocarpus* and *Geothallus* than to the higher forms of the Jungermanniaceae. . . . . Thus it seems that *Fossombronia longiseta* forms a connecting link between such forms as *Sphaerocarpus* and *Aneura*.

The development of the archegonium presents no striking difference from the usual situation; 6 neck canal cells are formed

and the venter becomes 2 cells thick only after fertilization. The first division of the fertilized egg is transverse, the upper segment forming the capsule and the lower forming the foot. The second transverse division separates the segment which is to form the capsule from that which is to form the seta. A third transverse division occurs in the uppermost cell, resulting in a tier of 4 superimposed cells. After this 2 vertical walls appear at right angles to each other, followed by periclinal walls in the upper segment. The author states that the capsule wall is normally 2 cells thick, but shows a wall composed of 3 layers of cells in his fig. 61. Both layers of the capsule bear annular thickenings. The mature elaters reach a length of 150–300 μ, and are provided with a double spiral thickening. Dehiscence is by means of four valves.

HUMPHREY's account of the development of the antheridium is vague, especially because no references to his figures are given in the description. Two interpretations are possible. If the second wall in the antheridium initial is transverse and is followed by vertical divisions in the two uppermost segments, the development is exactly like "what occurs in the majority of the Jungermanniaceae," as his figure representing this stage is the same as my fig. 11, except that the first vertical divisions result in an octant of cells instead of the condition shown in fig. 15. If HUMPHREY speaks of the initial as the dorsal segment resulting from the first transverse division of the true initial, then the third wall in the true initial is transverse instead of vertical, but the situation according to this interpretation would be precisely the same as that in *Sphaerocarpus*.

At any rate, HUMPHREY's series of stages are not sufficiently close to convince one that the situation in *Fossombronia* is radically different from that characteristic of most of the other Jungermanniales, and inasmuch as no mitotic figures are shown to prove the exact sequence of the first divisions in the initial, except for his figures of cross-sections, it is possible to interpret the development of the antheridium of *F. longiseta* as strictly normal. If HUMPHREY is really familiar with the development of the antheridium in the majority of the Jungermanniales as well as that of *Sphaerocarpus*, and the difficulty in interpreting his account is merely the result

of his obscurity in explaining the situation, the development of the antheridium would be as represented in fig. 1.

Investigation

Thallus

The vegetative body of *Fossombronia cristula* is minute, being only 2–4 mm. in length. It is creeping and semi-prostrate, although

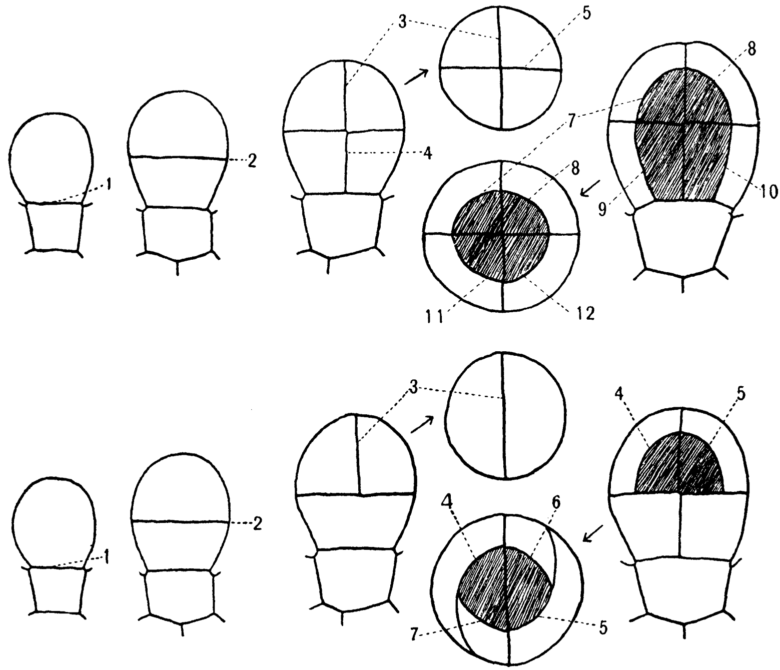

FIG. 1.—Above, *F. longiseta;* below, *F. cristula*

the stem tips may occasionally be more or less ascending. The branching is rather profuse and is strictly apical. The stem shows no indication of a conducting system as in *Pallavicinia* and *Symphyogyna*. The plants form dense matlike growths over the substratum, and are attached by means of long, violet-red rhizoids (fig. 6). The plant is an annual, developing in the early summer as soon as its habitat becomes sufficiently dry; in the Dune Park region the spores are ripe by late September or early October.

Growth of the main axis and branches is by means of a dolabrate (zweischneidig) apical cell (figs. 4, 5), with which are associated simple ventral mucilage hairs (figs. 7, 22) which may be several cells in length. CAVERS (2) states that each lateral segment of the apical cell of *Fossombronia*, by 2 transverse divisions, forms 3 horizontal cells, the upper and lower cells developing the stem and the middle cell forming a leaf, according to the same method as occurs in *Blasia*.

The leaves are borne in 2 dorsal rows; they are more or less erect, obliquely inserted on the stem, closely imbricate, and pale green (fig. 2). The ventral surface of the thallus is entirely devoid of leaves. HILL (5) notes that the leaves become paler and whitish with age. The shape of the leaves varies from somewhat quadrate to slightly obovate; they are very crisped and have subentire margins which occasionally bear a few feeble crenulations at the apex.

The cells of the stem and leaves contain numerous small peripheral chloroplasts. Considering the small size of the plant, the cells are relatively large. Mitotic divisions were very rare in the material studied; the best mitosis seen was that of a late metaphase in the apical cell (fig. 3). From a study of this figure it was estimated that the haploid number of chromosomes is 4, although this fact cannot be stated with absolute certainty, as no other stages of mitosis equally favorable for chromosome counting were found.

There can be no doubt that the 2 rows of lateral outgrowths from the axis of *Fossombronia* represent true leaves. The development of such a plant body from a form like *Pallavicinia Lyellii*, which consists of a midrib with thin, one-layered lateral wings slightly undulate on the margins, is very logical. *Symphyogyna aspera* might be taken to illustrate a second evolutionary stage, as in this plant the wing margins of the thallus are distinctly lobed. Among the Codoniaceae, *Blasia* represents a still farther advance, as in this case the lobes are even more distinct and regular, and the step from this condition to that of *Fossombronia* is perfectly natural. The plant body of *Noteroclada* is still more distinctly leafy, and in *Treubia* the axis bears 3 rows of leaves formed by an

apical cell of the pyramidal type. This series, of course, is not a truly phylogenetic one, but represents a sequence of hypothetical stages through which the Jungermanniaceae acrogynae have probably passed in the course of their evolution.

SEX ORGANS

The plants of *Fossombronia cristula* are monoecious; the sex organs are dorsal and scattered over the stem in the leaf axes. The antheridia and archegonia are more or less separately grouped, but both kinds may occur in the same leaf axis (figs. 7, 8). There is no time relation in the appearance of the sex organs; antheridia may precede or follow the archegonia, and this sequence may be repeated several times in any order.

The question of the differentiation of sex in *F. cristula* is an interesting one. Inasmuch as the thallus is bisexual and there is no definite sequence of antheridia and archegonia, sex must be determined at some other point in the life history than at the reduction division, or at one of the divisions of the apical cell. Up to the formation of the first horizontal wall in the initial, no differentiation of sex has occurred. Moreover, as the first vertical wall determines the kind of sex organ to be produced, sex probably is determined at the division concerned with the formation of the first gametogenous cell. It would be an interesting experiment to attempt to control sex in this plant by external conditions, as the sex organ initials probably contain the possibilities of both sexes.

ANTHERIDIUM.—The antheridia develop in small groups, either separately or with archegonia, in acropetal succession from the immediate dorsal segments of the apical cell. Each group comes to lie in the axis of a leaf which acts as an involucral organ, protecting the group from behind. There is no special involucre developed, as in many of the strictly thallose Jungermanniales, for, as the writer has pointed out in his study of *Pallavicinia* (4), the antheridial involucre of the thallose forms is strictly homologous with the involucral leaf of the foliose forms.

In the development of the antheridium of *F. cristula*, the initial becomes papillate (fig. 9), and by a transverse division a basal cell is cut off from an outer cell. A second transverse wall

then divides the outer cell into equal segments, forming a primary stalk cell and a primary antheridial cell (fig. 10). The next division is vertical in the antheridial cell, and is usually followed by a similar division in the stalk cell (fig. 11), which may be parallel with or at right angles to the vertical wall in the antheridial cell (figs. 13, 14). Two periclinal walls then appear in the antheridial cell (figs. 13, 14); their relation to the first vertical wall may best be seen in a cross-sectional view (fig. 15). Two additional periclinal walls, which come in at right angles to the first two, complete the peripheral layer of 4 primary wall cells, which are thus separated from the 2 central spermatogenous cells (fig. 15). The cell contents of the primary spermatogenous cells assume a much darker stain than the contents of the primary wall cells or the cells of the stalk; in no cases were periclinal walls seen in the stalk cell. Thus there can be no doubt that the antheridium develops according to the usual method found among the anacrogynous Jungermanniales, and not as HUMPHREY has described for *F. longiseta.*

Occasionally a transverse wall may appear in the stalk cell before the periclinal walls are formed in the antheridial cell (fig. 12), but usually the divisions of the stalk cell follow the formation of the primary wall cells. Sometimes, also, the first division of the stalk cell may be transverse instead of vertical (fig. 16). Further development of the spermatogenous tissue is like that of the other Jungermanniaceae anacrogynae. The stalk of the mature antheridium is commonly 4 cells in length, and invariably shows 4 cells in cross-section. The sperms are very small, slender, and extremely coiled before their escape from the antheridium. Each bears a pair of long terminal cilia. The sperms are produced in pairs from the sperm mother cells, but their development is not favorable for critical cytological study because of their extremely small size.

ARCHEGONIUM.—The archegonium originates from a papillate initial which may be formed from the first segment of the apical cell (figs. 21–23). This feature brings *Fossombronia* very close to the acrogynous Jungermanniales. In no case was an archegonium seen arising directly from the apical cell; consequently its activities are not checked by the production of sex organs.

The first wall of the initial is transverse, and comes in above the general level of the thallus, resulting in the formation of a basal cell and an outer cell (figs. 22–24). The former may undergo another transverse division immediately, or it may remain undivided until the 3 vertical walls have appeared in the outer cell (fig. 26). The presence of 2 transverse walls in the young archegonium caused the writer, during the early part of the investigation, to suspect that possibly the first transverse division of the initial is followed by a second one in the outer cell before the coming in of the 3 vertical walls. Archegonia were seen, however, in which only one transverse division of the initial had taken place (fig. 25), and the indications were that the development of the archegonium may be typical, or that the first 2 divisions of the archegonium initial may be the same as the first 2 of the antheridium initial (fig. 10).

Before the appearance of the first vertical wall, archegonia cannot be distinguished from antheridia, and after the first vertical wall has appeared the mitotic figure which would settle this point has disappeared. In several cases, however, the wall in the basal cell had not become thickened. This fact, together with the general aspect and behavior of the neighboring cells of the thallus, the position of the first wall in the initial, and the elongated character of the undivided stalk cell, convinced the writer, after a study of all available stages in the preparations, that the second transverse wall comes in the basal cell and not in the outer cell.

Subsequent development of the archegonium agrees with the usual development of the archegonium of anacrogynous forms (figs. 27–31). The cover cell divides by a median vertical wall soon after its formation (fig. 29), and remains in this condition; thus it does not contribute to the development of the neck, the cells of which in all cases increase by intercalary divisions. The mature archegonium has 6–8 neck canal cells, surrounded by 5 rows of neck cells (fig. 32). The venter is 2 cells in thickness, and slender, and the neck but slightly twisted. The ventral canal cell and egg are almost equal in size (fig. 31). After the breaking down of the axial row the protoplast of the egg is withdrawn somewhat from its wall, the very dense chromatin is in close contact with the nucleolus, and elongated slender plastids

are conspicuous in the cytoplasm (fig. 33). The egg protoplast does not lay down a new wall until after fertilization. More than one archegonium in a group may function (fig. 45).

That the archegonium is of an advanced type is shown by its early development from the initial, its relatively few neck canal cells, its inactive cover cell, the intercalary growth of the neck, and its slender venter.

Sporophyte

The first division of the fertilized egg is invariably transverse, and is followed by transverse divisions up to 5–7, the sequence of which could not be determined (figs. 34–36). A vertical wall then appears, intersecting the transverse walls (fig. 37), and followed by another vertical wall at right angles to the first one, so that 4 cells are seen in cross-section. Periclinal walls then appear in the upper part of the embryo and a sterile wall is thereby cut off from the central primary sporogenous cells. The relation of the early divisions of the embryo to the formation of the foot, seta, and capsule could not be determined, but it is certain that the lower half of the fertilized egg contributes to the development of the sporophyte, not merely forming an appendage to the foot. A slender calyptra 3 or 4 cells in thickness is formed from the venter of the archegonium (figs. 35, 38). A simple, bell-shaped involucre develops after fertilization; it slightly exceeds the sporophyte in length (fig. 45).

The sporogenous tissue is differentiated early in the history of the sporophyte. In the formation of the spore mother cells and elaters, the protoplasts of the sporogenous tissue withdraw from their cell walls (fig. 39), those which are to form spores round out, and both the spore mother cells and young elaters form a new wall as the original walls of the sporogenous mass are dissolved (fig. 40). The spore mother cells and young elaters are derived from the sporogenous cells by the same number of cell divisions. In *F. cristula* an elater is not homologous with a row of spore mother cells, as in forms with a more highly specialized sporophyte, but with a single spore mother cell. The spore mother cells develop 4 inconspicuous lobes (fig. 42), the reduction divisions

occur, and walls come in to separate the 4 members of the tetrad (fig. 43).

The material available for the investigation yielded no stage beyond that shown by fig. 44. No spiral thickenings were visible on the wall of the elaters, and the spores were in various stages of separation from their tetrads. The seta at this stage is not yet elongated. EVANS (3) has made a careful study of the mature spores and elaters of this species. He says:

> The elaters . . . . are remarkable not only on account of their small size and delicate structure but also on account of their variability in form and scanty development. Their most usual features, however, are found in the local thickenings on their walls. Instead of forming 2 or more parallel spirals, these usually consist of from 5 to 9 rings, some of which may be connected to form a single rudimentary spiral. . . . . The elaters vary from 28 μ to 50 μ in length and from 6 μ to 18 μ in width. The bands of thickening are less deeply pigmented than in most species of *Fossombronia* and are sometimes very pale indeed and difficult to demonstrate. . . . . The brown spores in the type material are mostly between 36 μ and 40 μ in diameter. . . . . The spherical face is covered over with a more or less regular reticulum formed by intersecting lamellae about 2 μ in height. . . . . The meshes of the reticulum are mostly 8–10 μ wide and the spherical face usually measures 6 or 7 meshes across. Sometimes the reticulum is irregular or incomplete.

The mature capsule is globular or nearly so; its wall is invariably 2 cells thick and bears rudimentary annular and half-ring fibers on the walls of the inner layer (fig. 46). There is no sterile cap at the apex of the capsule. Dehiscence, according to CAVERS (2), is by means of 4 valves in some species of *Fossombronia*, but in most of them the upper part of the capsule breaks into plates which are cast off irregularly.

Summary

1. The vegetative body of *F. cristula* consists of a minute, creeping, rather profusely branched thallus which bears genuine leaves in 2 dorsal rows.

2. The apical cell is dolabrate. Branching is strictly apical.

3. The plants are monoecious, the sex organs occurring in the axes of the leaves. Antheridia and archegonia may occur in the same leaf axis, and there is no time relation in the order of their

appearance. They originate from the immediate segments of the apical cell, and their development is strictly acropetal.

4. The antheridia develop according to the usual method found among the anacrogynous Jungermanniales. Variations occur in the order of appearance of the walls in the primary stalk cell.

5. Until the appearance of the first vertical wall, young archegonia cannot be distinguished from young antheridia. The first transverse division in the archegonium initial separates the stalk cell from the archegonium proper, and subsequent development follows the usual Jungermanniales type. The cover cell is inactive, 6–8 neck canal cells are formed, and the venter is 2 cells thick before fertilization. The archegonium is of an advanced type.

6. The early divisions of the embryo are transverse, both halves of the fertilized egg contributing to the development of the foot, seta, and capsule. A calyptra 3–4 cells in thickness is formed.

7. The sporogenous tissue is differentiated rather early in the history of the sporophyte. The elaters are rudimentary, and each is homologous with a single spore mother cell, not with a row of them.

8. The sporophyte is primitive.

To Dr. W. J. G. LAND, under whose direction the study was made, the writer makes grateful acknowledgment for his kind advice and helpful criticism.

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EXPLANATION OF PLATES XVI–XIX

PLATE XVI

FIG. 2.—Thallus: *a*, side view; *b*, dorsal view.

FIG. 3.—Mitosis in apical cell; ×1850.

FIG. 4.—Median longitudinal section of apical cell; ×660.

FIG. 5.—Median transverse section of same; ×660.

FIG. 6.—Rhizoids; ×85.

FIG. 7.—Median longitudinal section of thallus through apical cell; ×250.

FIG. 8.—Same as fig. 7: *a*, young antheridium; *lf*, leaf; ×68.

PLATE XVII

FIGS. 9–20.—Stages in development of antheridium.

FIG. 9.—Antheridium initial; ×790.

FIG. 10.—Young antheridium consisting of basal cell, stalk cell, and primary antheridial cell; ×790.

FIG. 11.—Vertical division of primary antheridial cell and later vertical division of stalk cell; ×790.

FIG. 12.—Appearance of transverse wall in stalk cell; ×790.

FIGS. 13–14.—Formation of periclinal walls in primary antheridial cell; ×790.

FIG. 15.—Cross-section of same; ×790.

FIGS. 16–17.—Division of primary wall cells; ×790.

FIG. 18.—Division of primary spermatogenous cells; ×790.

FIGS. 19–20.—Older stages; ×660.

FIG. 21.—Archegonium initial and apical cell; ×625.

FIG. 22.—First division of archegonium initial, apical cell, and mucilage hair; ×625.

FIGS. 23–33.—Stages in development of archegonium.

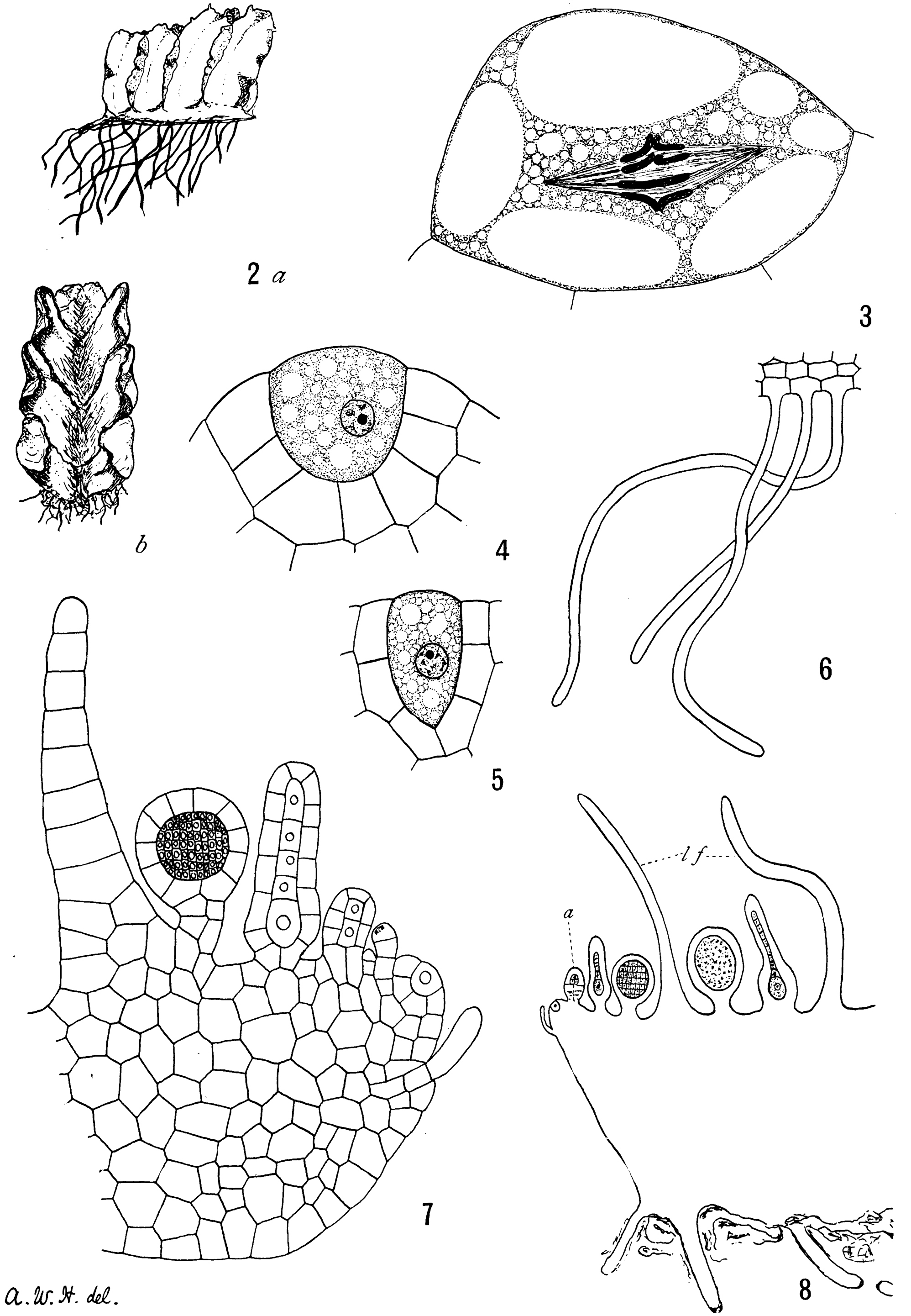
FIG. 23.—Archegonium initial; ×790.

PLATE XVIII

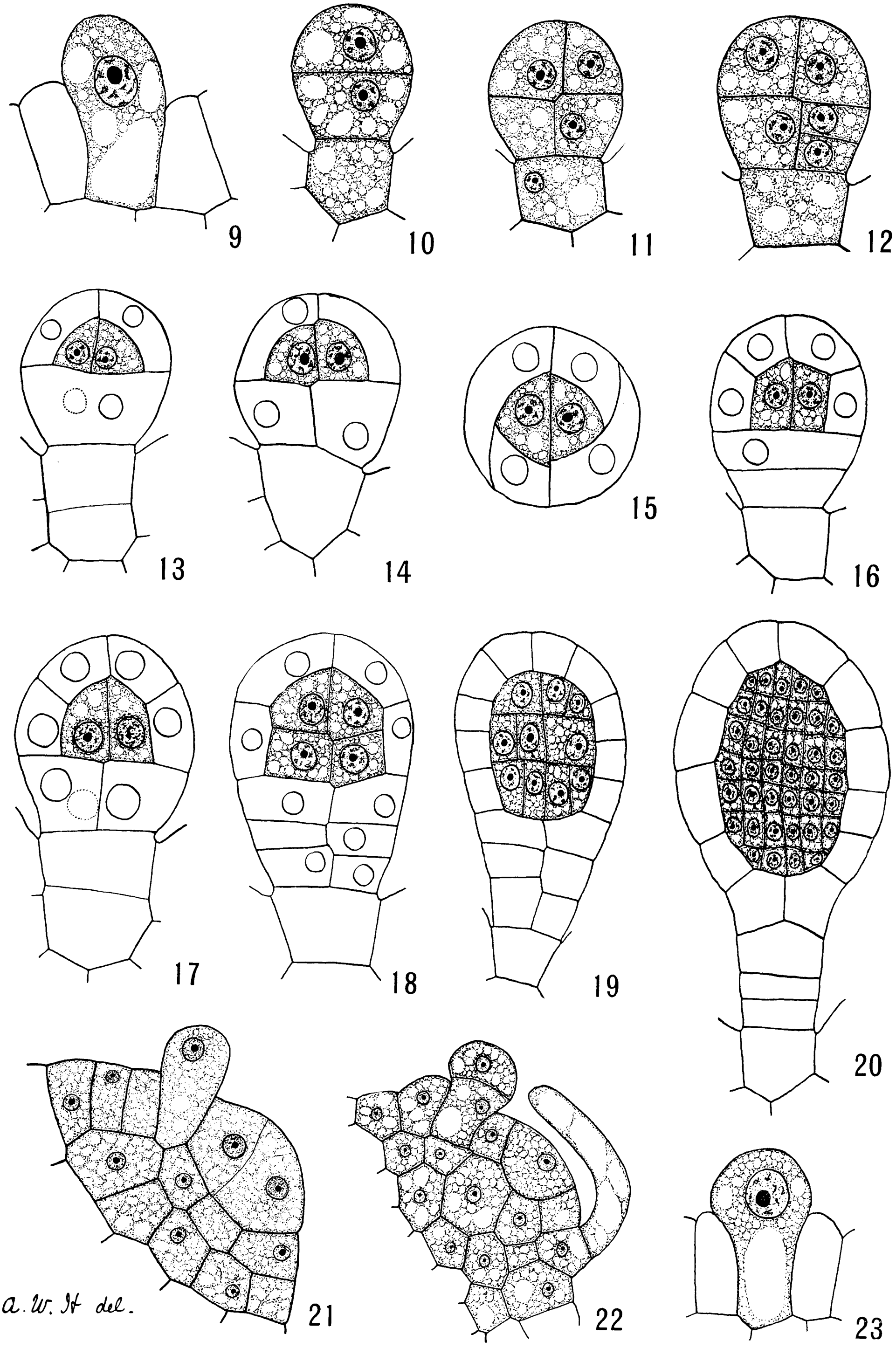
FIG. 24.—First division of same; ×790.

FIG. 25.—Formation of first vertical wall; ×790.

FIG. 26.—Appearance of second and third vertical walls and transverse division of basal cell; ×790.



HAUPT on FOSSOMBRONIA



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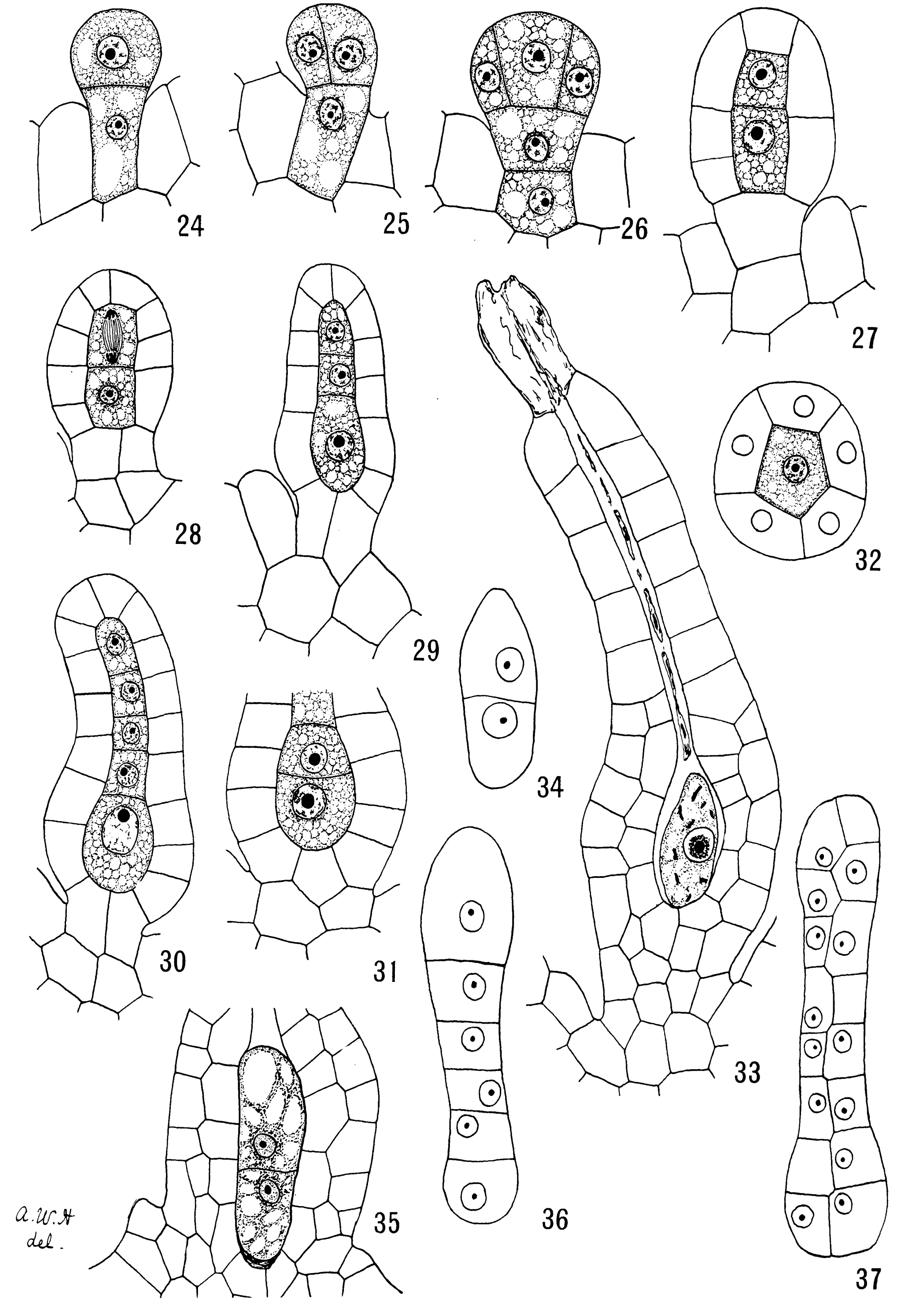

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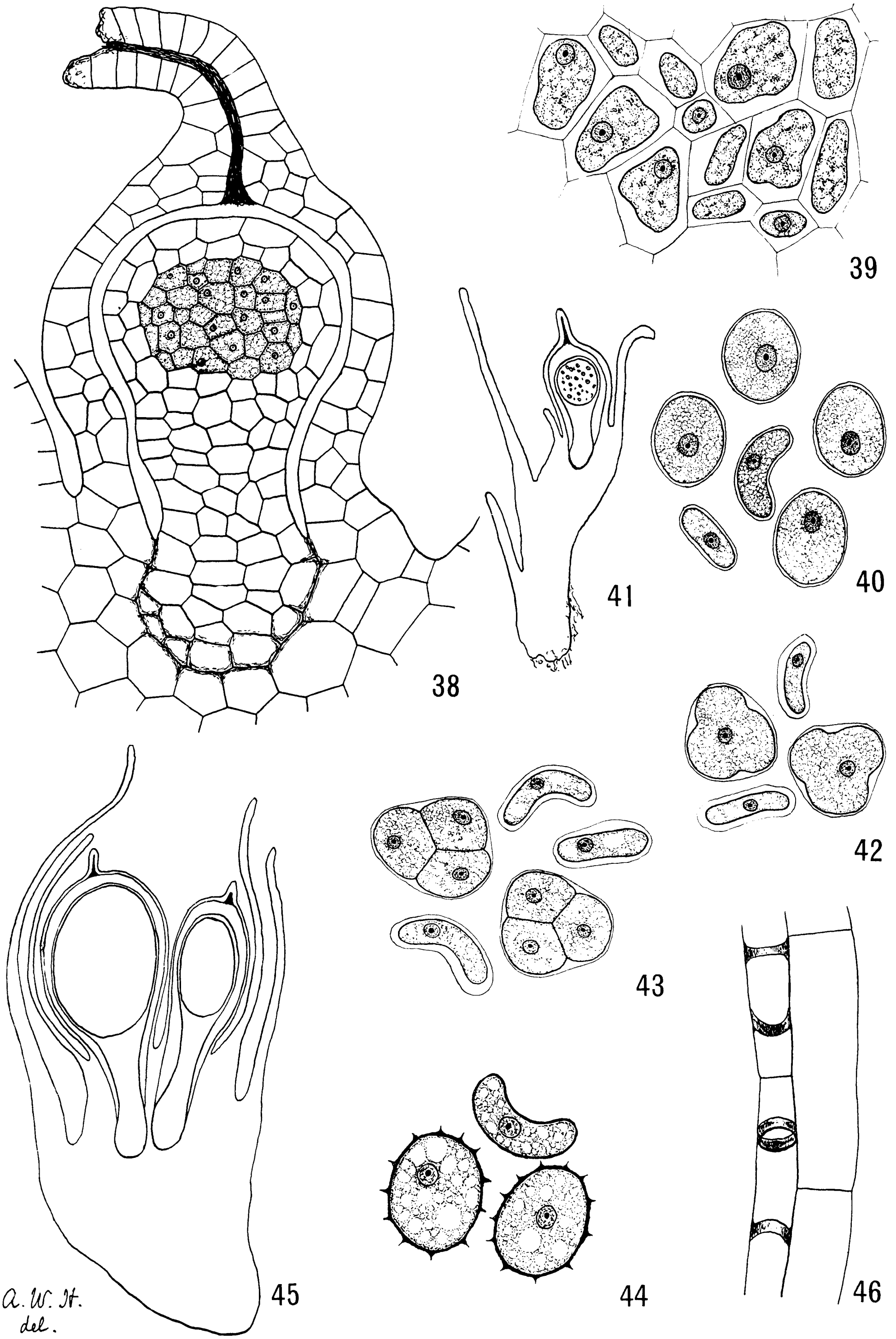

HAUPT on FOSSOMBRONIA

FIG. 27.—Young archegonium consisting of primary ventral cell, primary neck canal cell, and cover cell; ×790.

FIGS. 28–30.—Formation of neck canal cells, ventral cell undivided; ×660.

FIG. 31.—Ventral canal cell and egg; ×660.

FIG. 32.—Cross-section of neck of same; ×660.

FIG. 33.—Mature archegonium; ×525.

FIGS. 34–37.—Development of embryo; ×525.

PLATE XIX

FIG. 38.—Young sporophyte; ×340.

FIG. 39.—Differentiation of spore mother cells and elaters; ×525.

FIG. 40.—Spore mother cells and elaters; ×525.

FIG. 41.—Sketch of same stage; ×50.

FIG. 42.—Lobed spore mother cells; ×525.

FIG. 43.—Spore tetrads; ×525.

FIG. 44.—Nearly mature spores and elater; ×525.

FIG. 45.—Sketch of same stage; ×50.

FIG. 46.—Wall of mature capsule showing thickenings on inner layer; ×790.